

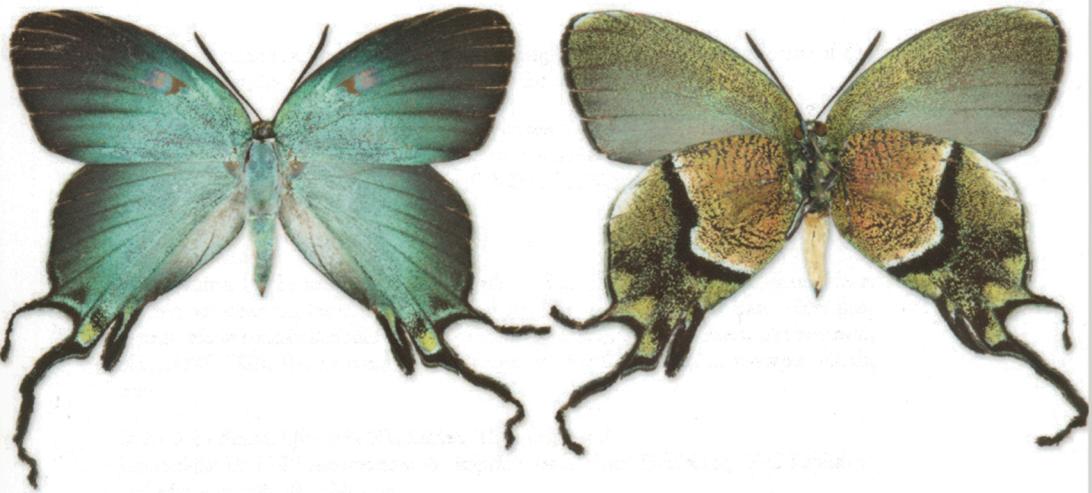
VOLUME 43 NUMBER 1 2012

ISSN 1399-560X / E-ISSN 1876-312X

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# Insect Systematics & Evolution

An International Journal of Systematic Entomology



Editor-in-Chief: Lars Krogmann

LEIDEN • BOSTON

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## Loss of male secondary sexual structures in allopatry in the Neotropical butterfly genus *Arcas* (Lycaenidae: Theclinae: Eumaeini)

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Published 20 March 2012

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### Abstract

Male secondary sexual characters in Lepidoptera may be present or absent in species that otherwise appear to be closely related, an observation that has led to differences of opinion over the taxonomic usefulness of these structures above the species level. An evolutionary issue raised by this debate is whether male secondary sexual characters (1) can be regained after being lost evolutionarily, (2) are not lost after being evolved, or (3) are 'switched on and off' by genes that regulate development. A second evolutionary issue is the conditions under which male secondary sexual characters might be lost or gained evolutionarily. Because these structures are thought to promote species recognition, theory predicts evolutionary losses to be most likely in allopatry; evolutionary gains to be most likely during the process of secondarily establishing sympatry or during sympatric speciation. We updated the species-level taxonomy of the brilliant emerald-winged Neotropical lycaenid butterfly genus *Arcas* and performed an analysis of phylogenetic relations among species to assess these evolutionary issues. We morphologically detail a scent pouch on the ventral hindwing of *Arcas* and report that six species possess the pouch with androconia, one possesses the pouch without androconia, and the remaining two species have neither pouch nor androconia. In addition, eight *Arcas* species have a morphologically species-specific male forewing scent pad, and one lacks a scent pad. This variation appears to be the result of three evolutionary losses and no gains of male secondary sexual organs. The four *Arcas* species lacking a scent pouch or a scent pad are allopatric with their closest phylogenetic relatives while four of five with both of these structures are sympatric. Although *Arcas* is a small genus, these results are significantly more extreme than predicted by chance. For taxonomy, this study provides a rationale for the evolutionary loss of male secondary sexual structures and suggests that their absence, but itself, does not indicate a lack of relationship above the species level.

### Keywords

Androconia, Dollo's law, sexual selection

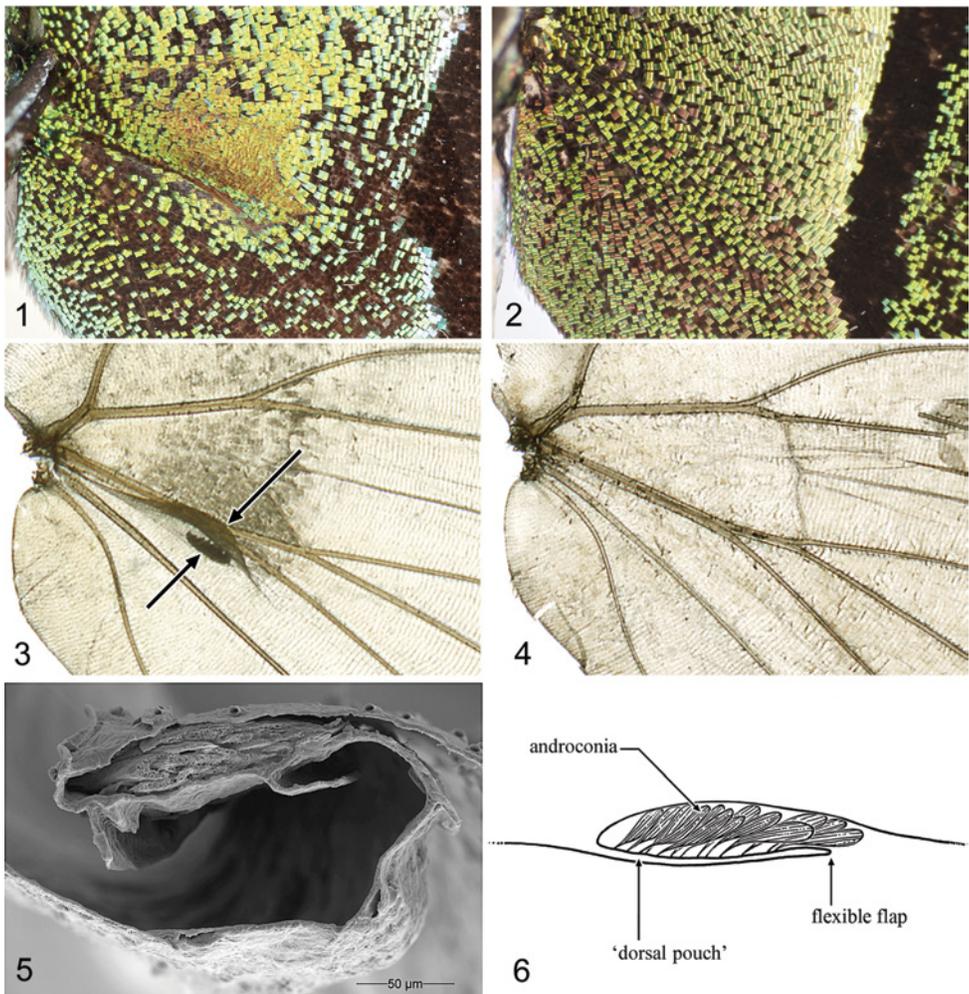
## Introduction

According to Eliot (1973: 399), “A curious feature of ... [male secondary sexual] characters is that they may be present or absent in closely related genera and species [of Lycaenidae]”. This pattern has been observed repeatedly in the taxonomic literature on Lepidoptera (e.g., Pierce 1909; Dixey 1910; Burns 1964; Stempffer 1967; Birch 1972; de Jong 1982 and included references), but the taxonomic use of male secondary sexual structures to characterize genera and other higher taxa has varied. At one end of the spectrum, these structures have been considered to be of minimal use for classification above the species level (e.g., Pierce 1909; Stobbe 1912; Stempffer 1967). For example, Pierce (1909: 19) concluded that ‘hair pencils’ in Noctuidae “are of no generic value”. More frequently, however, male secondary sexual structures have been treated as phylogenetically useful (e.g., Godman & Salvin 1887–1901; Swinton 1908; Ackery & Vane-Wright 1984; Boppré & Vane-Wright 1989; Hall & Harvey 2002; Willmott & Freitas 2006). The biological issue underlying the way that taxonomists have treated male secondary sexual characters is how these structures evolve.

According to Dollo’s Law, characters such as male secondary structures may be lost evolutionarily, but would then not re-evolve. The idea is that complex structures are unlikely to evolve ‘de novo’ exactly the same way twice (see Gould 1970 for a historical perspective on Dollo’s Law). At the other extreme, Bálint (2006: 149) argued that evolving a scent pouch (a male secondary structure) “is most probably costly” and expressed the view that if it “appeared in a lineage the character was never lost”. More moderately, it has been theorized that these intricate secondary sexual organs would not re-evolve ‘de novo’, but that genes that regulate their development might ‘switch them on and off’ evolutionarily (Burns 1964: 196–197; de Jong 1982: 695). Other than Quental (2008), the frequency of these alternate modes of evolution of male secondary sexual characters in Lepidoptera does not seem to have been assessed.

Male secondary sexual characters in insects are postulated to promote species recognition and to contribute to reproductive isolation among sympatric species (e.g., Löfstedt et al. 1991; Symonds & Elgar 2008). In accord with this idea, geographic patterns of pheromone character displacement are correlated with patterns of sympatry in Lepidoptera (Gries et al. 2001; McElfresh & Millar 2001; Groot et al. 2006; but see Symonds & Elgar 2004 for a bark beetle counterexample). More specifically, as proposed by Phelan and Baker (1987), a species that is allopatric with its closest relatives might lose a male secondary sexual character because reproductive isolation would not be an issue. Further, a species that loses a male secondary sexual character would be more likely to remain allopatric because it would be less likely to be able to maintain reproductive isolation if it secondarily became sympatric with its closest relatives. Alternately, secondarily becoming sympatric with a close relative or sympatric speciation are the kinds of situations in which a new male secondary structure might evolve. Evidence supporting these expectations has been reported in moths (Phelan & Baker 1987).

In a discussion of male secondary sexual structures in Central American Lycaenidae (Lepidoptera: Theclinae: Eumaeini), Godman and Salvin (1887–1901) reported that



**Figs 1–6.** Scent pouch morphology in *Arcas*. (1) Pouch opening on ventral surface of hindwing (*A. cypria*, Panama). (2) Pouch lacking on ventral surface of hindwing (*A. tuneta*, Peru). (3) Pouch in cleared wings (*A. cypria*, Panama), arrow at top points to the flexible flap of the pouch, arrow at bottom to the androconia. (4) Pouch lacking in cleared wings (*A. tuneta*, Brazil, SC). (5) SEM cross-section of hindwing pouch (*A. imperialis*) showing the position of the androconia, dorsal surface at top. The height of the 'dorsal pouch' is an artifact of preparation. (6) Drawing of the cross-section of hindwing pouch (*A. imperialis*), dorsal surface at top. This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

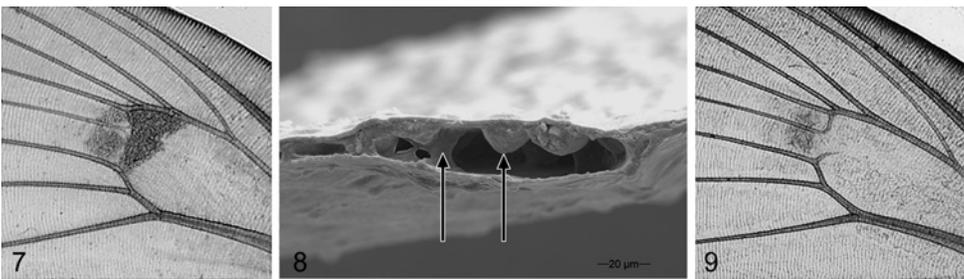
some males have a pouch or fold in the membrane on the ventral surface of the hindwing (Figs 1–6). This pouch has been reported in species now placed in *Pseudolycaena* Wallengren, *Theritas* Hübner, and *Arcas* Swainson (Godman & Salvin 1887–1901, Bálint 2006) — all members of the *Atlides* Section of the Eumaeini (a group of four genera, Robbins 2004). Eliot (1973) noted specialized scales in the pouch, but the pouch structure has otherwise not been detailed. Finally, Eliot (1973: 402) wrote

“The means of scent diffusion from this pouch is a mystery to me, since there are no associated hair brushes ... nor apparent wing musculature which could evert it ...”

In addition to ventral hindwing scent pouches, many males in the *Atlides* Section of the Eumaeini also have forewing scent pads. Eumaeine scent pads differ from other male scent organs by separated wing membranes that form a cavity with supporting columns and with invaginations on the dorsal wing surface that contain a secretory cell and the base of an androconium (Figs 7–9, see Thomas 1893 for histology, Robbins 1991 for SEM micrographs). Species of *Arcas*, *Theritas*, *Atlides* and *Pseudolycaena* may possess both forewing scent pads and hindwing scent pouches, only scent pads, only scent pouches, or neither, indicating that these male secondary sexual structures have been gained and/or lost evolutionarily, so it would appear to be an appropriate group of insects in which to study the evolution of male secondary sexual characters.

The strikingly brilliant emerald-green wings and long tails of *Arcas* make it one of the most readily recognizable hairstreak genera in the world (Figs 28–32), and it was one of the first Neotropical lycaenid genera to be revised taxonomically (Nicolay 1971). In the past 40 years, the monophyly of *Arcas* as delimited in Nicolay has not been disputed, and the only modification of the species level classification from Nicolay’s classification is that *A. splendor* is now treated as three geographically allopatric species (results below). However, neither Nicolay’s paper nor subsequent taxonomic papers on *Arcas* addressed phylogenetic relationships within the genus (Austin & Johnson 1995; Salazar & Constantino 1995a,b; Johnson & Salazar 2002; Bálint 2002, 2006; Salazar 2004; Bálint & Wojtusiak 2006).

The purpose of this paper is to assess the evolution of male secondary sexual structures in *Arcas*. To accomplish this goal, we update the species-level taxonomy of *Arcas* and summarize information on the variation, biogeography, ecology, and behavior of each *Arcas* species. We also describe the morphology of Godman and Salvin’s (1887–1901) hindwing scent pouch and suggest how it disseminates scent. Finally, we infer phylogenetic relations among the species of *Arcas*, map the evolution of male secondary sexual structures on the resulting cladogram, and discuss the evolution of these structures in relation to allopatry and sympatry.



**Figs 7–9.** Scent pad morphology in *Arcas*. (7) One scent pad in the discal cell and one distal of the discal cell (*A. imperialis*). (8) SEM cross section of discal cell scent pad showing the separated wing membranes supported by columns (arrow on left) and the pouches that contain scent cells and the base of androconia (arrow on right, *A. imperialis*). (9) A single scent pad distal of the discal cell (*A. tuneta*).

## Materials and Methods

The species level taxonomy of *Arcas* is updated from that of Nicolay (1971) and succeeding authors primarily by analyzing the geographical variation of proposed distinguishing traits. In one case, we split a montane taxon into three allopatric species because there is no geographical variation in the characters that distinguish these taxa. In another, we lump named lowland populations because their distinguishing traits are variable and overlapping. We do not use the subspecies category following the reasons in Wilson and Brown (1953). A corrected nomenclatural list and male identification key are presented. For morphological structures, wing vein names follow Comstock (1918), androconial terminology follows Robbins (1991), and other morphology follows Snodgrass (1935).

To measure aspects of wing venation, pattern, and shape from specimen images, we used the measure tool of Adobe Photoshop<sup>®</sup>. Specifically, to distinguish females of *A. gozmanyi* and *A. splendor* (Fig. 30), we calculated proportions, which were normalized using an arcsine transformation (Sokal & Rohlf 1969: 386). We calculated statistics and did a standard t-test on the arcsine transformed variables using commercially available SAS software. We report the sample statistics and 95% confidence intervals after transforming the results back to proportions.

The length of the third segment of the labial palps was measured with an ocular micrometer.

Information on distribution, larval food plants, male behavior, and habitat are taken from the literature, from vouchers in the museum and private collections listed below, from our field work, and from the field notes of G.B. Small Jr., which are deposited in the USNM (museum abbreviations listed below). Biogeographical zones follow Brown (1982), who partitioned the forested continental Neotropics into the Transandean Region, Andean Region, Amazon Region, and Atlantic Region. Larval food plant nomenclature follows the Tropicos database of the Missouri Botanical Garden ([www.Tropicos.org](http://www.Tropicos.org), accessed November 2010). Food plant common names were identified from Grandtner (2005). Following Elias et al. (2009), we classify *Arcas* species as lowland (0–1200 m), lower montane (500–1700 m), or montane (> 1300 m). Following Holdridge (1967), we classify lowland forests as humid/wet (> 200 cm annual precipitation) or dry/deciduous (100–200 cm annual precipitation). Many butterflies, including eumaeines, display male territorial behavior (Nicolay 1971, Alcock & O'Neill 1986, 1987, Cordero et al. 2000 for examples from the Eumaeini), often on hilltops (Shields 1967, Scott 1970). Males wait on hilltops for receptive females to fly through the territory and 'defend' these areas by flying at other males that enter the territory. Recorded times from our fieldwork for hilltopping behavior are the standard time at that locality. Finally, traps baited with decaying fish attract some lycaenid species and not others. We note species, gender, and standard time at that locality for each specimen collected using fish-baited traps.

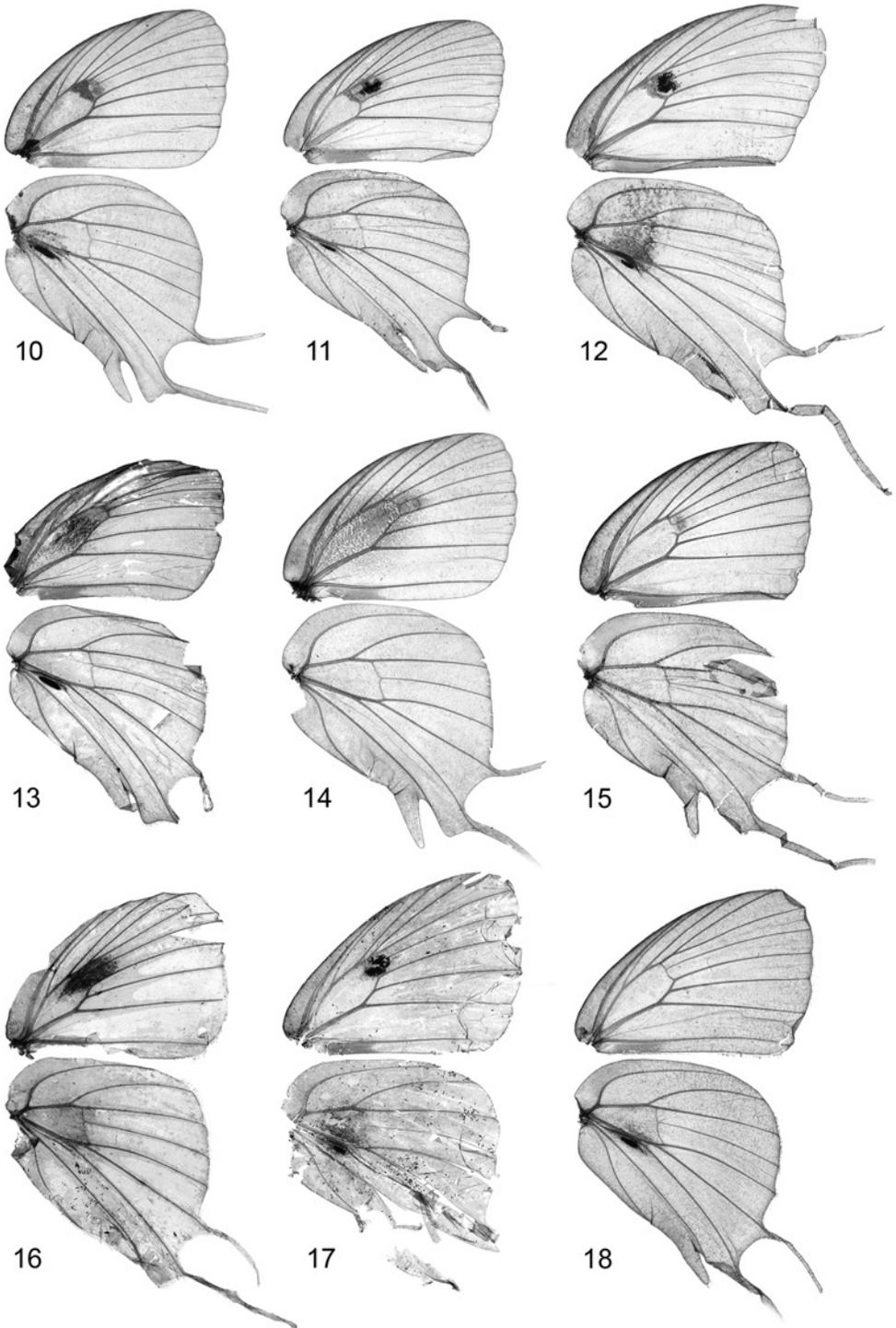
Characters for the phylogenetic analyses were based on adult morphology because the only specimen voucher for an *Arcas* immature is a pupal case of *A. ducalis* (Zikán 1956) and because DNA sequences are currently available for only two species

(Quental 2008). We found phylogenetically informative characters in the scent pads, scent pouches, pattern, venation, and shape of the wings. Wing slides were made for 22 *Arcas* adults (plus additional preparations for the outgroups) and digitized following standard methods (Robbins & Duarte 2005, Figs 10–18). To study scent-producing and disseminating structures using an SEM, we prepared wing cross-sections following the methods in Robbins (1991). We also dissected hindwing scent pouches under a binocular microscope. Nicolay (1971) was unable to distinguish species solely on the basis of genitalic structures, and accordingly, we found no interspecific genitalic variation that could be coded.

Nine *Arcas* species are recognized (Table 1). Eight were previously listed (Robbins 2004), but based on results in this paper, one name is removed from synonymy and two have their nomenclature altered. The outgroups for the cladistic analysis are *Theritas mavors* (Hübner) and *T. triquetra* (Hewitson). *Arcas* and *Theritas* were placed in the *Atlides* Section of the Eumaeni (Robbins 2004), and Bálint (2006) suggested that *Theritas* is a close relative of *Arcas* because they have similarly sized hindwing pouches. Furthermore, a phylogenetic analysis of molecular data supports a sister group relationship between *Theritas* and *Arcas* (Quental 2008).

Character states for each *Arcas* and outgroup species (Table 2) were recorded in Nexus Data Editor (software from R.D.M. Page, taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html) (Table 2). We searched exhaustively for shortest trees using the implicit enumeration option of TNT software (Goloboff et al. 2008) to derive a most parsimonious cladogram with the collapse trees after the search option. To test the assumption of equally weighted characters, implied weighting was performed over a range of values for the parameter  $K$  (1, 10, 50, 250 and 1000). Characters were analyzed non-additively. Mapping of characters on trees was done with WinClada software (Nixon 2002) with the unambiguous changes only options. Bootstrap support was determined in WinClada (1000 replications with mult\*10, memory 1000 trees). The presence or absence of hindwing scent pouches, androconia in the pouches, and forewing scent pads was optimized on the cladogram.

We tabulated for each species whether it has one or two wing androconial types (scent pad, scent pouch) and whether it is sympatric or allopatric with its sister lineage (Table 3). Traditionally, to test the null hypothesis that these two factors are independent, a goodness-of-fit test on the contingency tables has been performed (e.g., Phelan and Baker 1987). This test assumes that each species is an independent sample, but this assumption is not met. For example, the lack of a hindwing scent pouch in *A. delphia* and *A. tuneta* is due to one evolutionary loss on the cladogram. Further, a concentrated changes test for correlated evolution (e.g., Maddison 1990, Lorch & Eadie 1999) is inapplicable because sympatry/allopatry is not a phylogenetic character. As an alternative, given the inferred tree structure and information on the sympatry or allopatry for each pair of species (in the species accounts), we determine how our results compared with those from a sample of 200 trees produced using the random shuffle of terminal taxa option of Mesquite software (Madison & Madison 2011) for the ingroup species. We calculated the distribution of the number of species that meet the expectation of theory from each of the 200 trees and estimated the  $P$ -value as the proportion that equaled or were more extreme than our results.



**Figs 10–18.** Digitized male wing slides. (10) *A. imperialis* (Colombia); (11) *A. ducalis* (Brazil, SC); (12) *A. cypria* (Panama); (13) *A. jivaro* (Bolivia); (14) *A. delphia* (Panama); (15) *A. tuneta* (Brazil, SC); (16) *A. gozmanyi* (Panama); (17) *A. splendor* (Ecuador); (18) *A. alleluia* (Peru).

**Table 1.** Character matrix for *Arcas*

|                           | Taxa |   |   |   |   |     |   |   |   |     |    |    |    |    |    |    |    |
|---------------------------|------|---|---|---|---|-----|---|---|---|-----|----|----|----|----|----|----|----|
|                           | 1    | 2 | 3 | 4 | 5 | 6   | 7 | 8 | 9 | 10  | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| <i>Theritas mavors</i>    | 0    | 0 | 0 | 0 | 0 | 0   | 0 | 0 | 0 | 0   | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Theritas triquetra</i> | 0    | 0 | 0 | 0 | 0 | 0   | 0 | 0 | 0 | 0   | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Arcas imperialis</i>   | 1    | 2 | 0 | 1 | 1 | 1   | 1 | 2 | 2 | 0   | 1  | 1  | 0  | 0  | 0  | 0  | 0  |
| <i>Arcas ducalis</i>      | 1    | 1 | 0 | 0 | 1 | 1   | 1 | 2 | 2 | 0   | 1  | 1  | 0  | 0  | 0  | 0  | 0  |
| <i>Arcas cypria</i>       | 1    | 2 | 0 | 0 | 1 | 1/2 | 1 | 2 | 1 | 0   | 1  | 1  | 1  | 0  | 0  | 0  | 0  |
| <i>Arcas jivaro</i>       | 1    | 1 | 1 | 1 | 1 | 2   | 1 | 2 | 1 | 0   | 0  | 0  | 0  | 0  | 0  | 1  | 0  |
| <i>Arcas delphia</i>      | 1    | 1 | 1 | 1 | 1 | 1   | 1 | 2 | 1 | 1   | 0  | 0  | 0  | 1  | 2  | 1  | 1  |
| <i>Arcas tuneta</i>       | 1    | 0 | 0 | 1 | 1 | 1   | 1 | 2 | 1 | 0/1 | 0  | 0  | 1  | 1  | 2  | 1  | 1  |
| <i>Arcas gozmanyi</i>     | 1    | 2 | 0 | 0 | 1 | 1/2 | 1 | 1 | 1 | 0   | 0  | 0  | 0  | 0  | 1  | 1  | 0  |
| <i>Arcas splendor</i>     | 1    | 2 | 0 | 0 | 1 | 1   | 1 | 1 | 1 | 0   | 0  | 0  | 0  | 0  | 0  | 1  | 0  |
| <i>Arcas alleluia</i>     | 1    | 2 | 0 | 0 | 1 | 1   | 1 | 1 | 1 | 0   | 0  | 0  | 0  | 0  | 0  | 2  | -  |

The outgroups are *Theritas mavors* and *T. triquetra*.

**Table 2.** Characters used in the phylogenetic analysis

1. Frons color: (0) Muted green-brown, (1) Gold-green.
2. Length of third labial palp segment in males: (0) <0.3 mm, (1) 0.45–0.75 mm, (2) >0.95 mm.
3. Length of discal cell (wing base to original of vein M2) to length of M2 (origin of M2 to its terminus): (0) <1, (1) >1.
4. Forewing vein R3: (0) Stalked, (1) Arises from discal cell.
5. Length of anal lobe cleft: (0) 1–3 mm, (1) >3 mm.
6. Male apical border on dorsal surface of forewing: (0) <3 mm, (1) 4–6 mm, (2) >6 mm.
7. Ground color of ventral surface of male wings: (0) Muted green-brown, (1) Emerald green scales.
8. Female postmedian line on ventral surface of forewing: (0) Brown, (1) Black (but may be vestigial), (2) None.
9. Color of female ventral hindwing postmedian line anterior of vein Cu1: (0) Brown, (1) Black, (2) None.
10. Pale iridescent postmedian “band” on ventral surface of the forewing in females: (0) Absent, (1) Present.
11. Basal part of hindwing on the ventral surface with semi-circular black striations (noted by Nicolay for *A. imperialis*): (0) Absent, (1) Present.
12. Shape of male dark postmedian line on ventral surface of hindwing from the inner margin to vein Cu1: (0) Curved, (1) Straight.
13. White scales at apex of hindwing on ventral surface: (0) Absent, (1) Present.
14. Pouch on ventral surface of hindwing in cell Cu2-2A: (0) Present, (1) Absent.
15. Androconia on ventral surface of hindwing: (0) Present, (1) A few scattered androconia, (2) None.
16. Scent pad on the dorsal surface of the forewing: (0) Double, (1) Single, (2) None.
17. Scent pad androconia in the discal cell: (0) Present, (1) Absent.

The collections from which we accumulated data on *Arcas* include American Museum of Natural History (AMNH), New York, NY, USA; Academy of Natural Sciences Pennsylvania (ANSP), Philadelphia, PA, USA; The British Museum of Natural History (BMNH), London, UK; Fundação Instituto Oswaldo Cruz (FIOC), Rio de Janeiro, RJ, Brazil; Smithsonian Institution, Jason Hall and Keith Willmott Collection

**Table 3.** Number of *Arcas* species that are allopatric or sympatric with their sister lineage versus the number of species that have one or two kinds of male secondary sexual structures

|            | Two kinds of male secondary sexual structures | One kind of male secondary sexual structures | Total     |
|------------|---|--|-----------|
| Sympatric  | 4 species                                     | 0 species                                    | 4 species |
| Allopatric | 1 species                                     | 4 species                                    | 5 species |
| Total      | 5 species                                     | 4 species                                    | 9 species |

Allopatric species with one kind of androconial structure plus sympatric species with two kinds (8 of the 9 species) occur more frequently than would be expected by chance (Randomization Test,  $P=0.015$ , see text).

(JHKW), Washington, DC, USA; Loran D. Gibson Collection (LDG), Florence, KY, USA; Harvard University, Museum of Comparative Zoology (MCZ), Cambridge, MA, USA; Universidad Nacional Mayor de San Marcos, Museo de Historia Natural (MUSM), Lima, Peru; Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, SP, Brazil; Oxford University Museum of Natural History (OUMNH), Oxford, UK; Robert C. Busby Collection (RCB), Andover, MA, USA; Smithsonian Institution, National Museum of Natural History (USNM), Washington, DC, USA.

## Systematics

### Key to male *Arcas* based on wing characters (Figs 1–32, figs 7–11 in Nicolay 1971)

1. Ventral hindwing with a black postmedian band, extending from the anal margin to the costal margin..... 3  
     Ventral hindwing without the anterior portion of the black postmedian band. The reduced black band is limited to the anal portion of the hindwing ..... 2
2. Ventral hindwing with a gold submarginal band ..... *A. ducalis*  
     Ventral surface of hindwing without a gold submarginal band..... *A. imperialis*
3. Anterior half of ventral hindwing black postmedian band strongly concave .....  
     ..... *A. cypria*  
     Anterior half of ventral hindwing black postmedian band relatively straight ..... 4
4. Dorsal forewing with androconia..... 5  
     Dorsal forewing without androconia ..... *A. alleluia*
5. Dorsal forewing scent pad crisply defined, androconia clearly visible ..... 6  
     Dorsal forewing scent pad and androconia with a diffuse, poorly defined appearance..... *A. jivaro*
6. Dorsal forewing scent pad oval in shape ..... 7  
     Dorsal forewing scent pad ‘tear-shaped’ ..... *A. gozmanyi*
7. Dorsal forewing scent pad located on the basal side of the midpoint of the forewing..... 8  
     Dorsal forewing scent pad located on the distal side of the forewing, just to the outside of an elongated discal cell..... *A. delphia*

8. Dorsal forewing scent pad located outside the discal cell and ventral hindwing with marginal white scales .....*A. tuneta*  
 Dorsal forewing scent pad located at the end of the discal cell (split: part inside and part outside) and the ventral forewing with a black postmedian band (highly variable from a complete band to just a few black scales) .....*A. splendor*

### Nomenclatural Checklist

*ARCAS* Swainson, 1832, type species: *Papilio imperialis* Cramer  
*Arcas imperialis* (Cramer, 1775) (*Papilio*), type locality: Surinam  
*actaeon* (Fabricius, 1775) (*Papilio*), type locality: ?, suppressed (ICZN, Op. 1058)  
*venus* (Fabricius, 1781) (*Papilio*), type locality: Surinam, repl. name  
*oakesii* (Butler, 1884) (*Theritas*), type locality: Colombia  
*magnifica* Austin & K. Johnson, 1995, type locality: Brazil (RO)  
*Arcas ducalis* (Westwood, 1852) (*Thecla*), type locality: Brazil  
*Arcas cypria* (Geyer, 1837) (*Theritas*), type locality: Mexico (YUC)  
*paphia* (C. Felder & R. Felder, 1865) (*Pseudolycaena*), type locality: Colombia  
*publica* (Röber, 1923) (*Thecla*), type locality: Colombia  
*Arcas jivaro* Nicolay, 1971, type locality: Ecuador  
*Arcas delphia* Nicolay, 1971, type locality: Costa Rica  
*katia* Salazar, 2001, type locality: Colombia, nom. nud.  
*katia* K. Johnson & Salazar, 2002, type locality: Colombia  
*Arcas tuneta* (Hewitson, 1865) (*Thecla*), type locality: (Brazil (AM))  
*marginata* Austin & K. Johnson, 1995, type locality: Brazil (RO)  
*viriditas* Austin & K. Johnson, 1995, type locality: Brazil (RO)  
*arcadia* Bálint, 2002, type locality: Brazil (SC)  
*Arcas gozmanyi* Bálint, 2006, type locality: Panama  
*Arcas splendor* (H.H. Druce, 1907) (*Thecla*), type locality: Colombia  
*nicolayi* Salazar & Constantino, 1995, type locality: Colombia  
*lecromi* Salazar & Constantino, 1995, type locality: Colombia  
*Arcas alleluia* Bálint, 2002, type locality: Peru

### *Arcas* Swainson

#### *Diagnosis*

Unique identifying traits for *Arcas* include a hindwing anal lobe cleft approximately 4 mm long and tails up to 15 mm in length coupled with rows of emerald colored scales on the ventral wing surfaces. Other synapomorphies that characterize *Arcas* in the phylogenetic results (unambiguous changes only, Fig. 35) are frons color gold-green, length of male third labial palp segment greater than 0.45 mm, male apical border on dorsal surface of forewing greater than 4 mm, female postmedian line on ventral surface of forewing lacking (a black postmedian line evolved secondarily within the genus according to the phylogenetic results), and color of female ventral hindwing postmedian line anterior of vein Cu<sub>1</sub> black. *Arcas* is a distinctive and highly apomorphic genus.

### *Wing shape* (Figs 10–18)

Thick tails up to 15 mm in length and a deeply cleft hindwing just basal of the terminus of vein 2A are characteristic of *Arcas*. The anal lobe cleft is deeper (approximately 4 mm in length) than in other Eumaeini, which may or may not have a cleft anal lobe (Godman & Salvin 1887–1901). The length and thickness of the hindwing tails distinguish *Arcas* from most other Eumaeini.

### *Wing venation* (Figs 10–18)

Forewing vein R<sub>3</sub> may be stalked (character 4). The forewing discal cell in *A. delphia* and *A. jivaro* is longer than in the other species (character 3). Otherwise, wing venation is similar among *Arcas* species, and sexual dimorphism is relatively negligible, in contrast to some members of the *Atlides* Section, such as *Theritas hemon* (Cramer).

### *Postmedian line on ventral surface of the forewing*

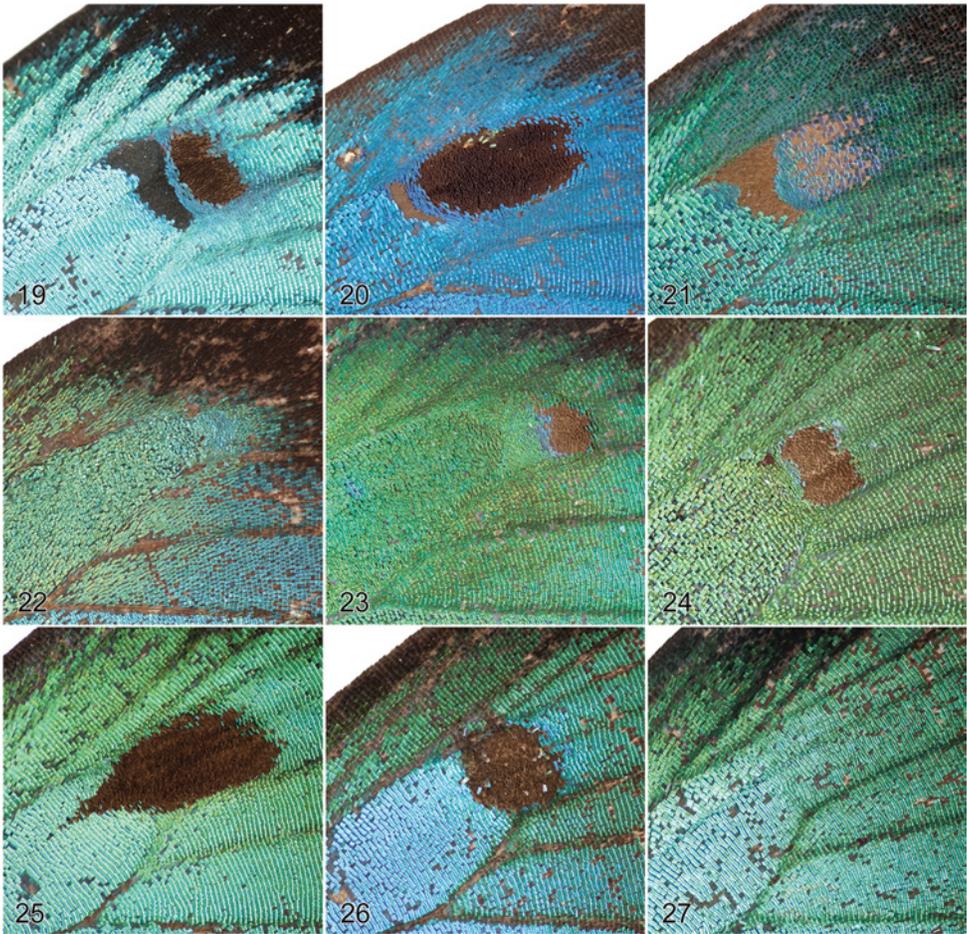
A postmedian line on the ventral surface of the forewing occurs in females of *A. gozmanyi*, *A. splendor*, and *A. alleluia* (Figs 30 and 31) and in males of *A. splendor* (Fig. 32). This line is poorly developed in smaller females of *A. gozmanyi*, where it may be reduced to a few black scales (Fig. 31). Our study series included only three females of *A. splendor* and two females of *A. alleluia*, which is insufficient to assess variability, but expression of this line is reduced in the illustrated female holotype *A. alleluia*, which is also smaller than the other females that we examined. The expression of this line in male *A. splendor* is also highly variable, but unlike females, it does not appear to be a function of size (Fig. 32). So far, every individual that we have examined of *A. splendor* and every female of *A. gozmanyi* and *A. alleluia* has had at least a few black scales (examined with a stereomicroscope) in the postmedian part of the ventral surface of the forewing.

### *Scent pads* (Figs 7–9, 19–27)

Scent pads have the wing membranes separated by supporting columns, forming an internal chamber with invaginations on the dorsal surface that contain a scent cell and the base of the androconium (Thomas 1883, Robbins 1991). As characterized, all male *Arcas* have a scent pad on the dorsal surface of the forewing except for *A. alleluia* (Fig. 27). In some species, the size and density of scent pad androconia in the discal cell are different from those distal of the discal cell (e.g., *A. imperialis*, Figs 7 and 19), giving the scent pad a double appearance (character 16, Figs 10–12). In others, there is no difference (e.g., *A. gozmanyi*) or the discal cell lacks a scent pad (e.g., *A. delphia*). The scent pad on the dorsal surface of the forewing in *A. jivaro* is covered with iridescent wing scales (Fig. 22), which gives the male the unusual appearance noted by Nicolay (1971).

### *Scent pouches* (Figs 1–6)

Godman and Salvin (1887–1901) first reported that the hindwing membrane is folded in cell Cu<sub>2</sub>-2A into a pouch (Figs 1–6) in some species now placed in the *Atlides*



**Figs 19–27.** Male scent pads on the dorsal surface of the forewing. (19) *A. imperialis* (Panama); (20) *A. ducalis* (Brazil, SC); (21) *A. cypria* (Panama); (22) *A. jivaro* (Bolivia, scent pad covered with iridescent wing scales); (23) *A. delphia* (Costa Rica); (24) *A. tuneta* (Brazil, SC); (25) *A. gozmanyi* (Panama); (26) *A. splendor* (Ecuador); (27) *A. alleluia* (Peru, scent pad lacking). This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

Section. The folded wing membrane forms a dorsal and ventral pouch (Fig. 6), each of which is lined with scales. The ‘dorsal’ pouch does not seem to have been previously noted.

The length and position of the hindwing pouch, when present, is interspecifically variable in the *Atlides* Section (Godman & Salvin 1887–1901, Bálint 2006, Fig. 3 for *Arcas*). The anterior edge of the pouch may be near the body (*Arcas* and *Theritas*) or just distal of the origin of vein  $Cu_2$  (*Pseudolycaena*). The distal edge of the ventral pouch may be just distal to the origin of vein  $Cu_2$  (*Arcas* and some *Theritas*) or well distal of it (some *Theritas* and *Pseudolycaena*).

When a male Eumaeini courts a female, he lands next to her and rapidly vibrates his wings (Powell 1968, Scott 1974, Lundgren & Bergstrom 1975, Robbins 1980), a behavior that has been reported only during courtship. Every time a live hand-held

male of *Theritas hemon* (Cramer) opened its wings, the ventral flap of the pouch (Fig. 6) also opened slightly exposing the androconia (Robbins unpubl.), which presumably allows scent to be disseminated when the wings are rapidly vibrated. More generally, this flap is flexible in live individuals, but rigid in museum specimens, which is probably why Eliot (1973) did not consider this possibility for scent dissemination. In lieu of other evidence, we presume that a flexible pouch allows scent to be disseminated in *Arcas*, even though the pouch is significantly smaller in *Arcas* than in *T. hemon*.

Androconia are attached at the distal end of the ventral surface of the ventral pouch (Figs 3,6). They are hollow scales with their tips oriented towards the opening of the pouch. The androconia vary in color from off-white to charcoal, with the androconia sometimes being charcoal basally and off-white distally. Males of *A. gozmanyi* possess the pouch, but lack androconia (Fig. 16), although it is possible that a few scattered scales in the pouch are vestigial androconia (four wing slides examined). Pouches that lack androconia have been reported in a variety of Lepidoptera (Birch 1970, Grant 1978). Males of *Arcas delphia* and *A. tuneta* lack the pouch and lack androconia where the pouch would be (Figs 2 and 4). Similarly, in *Psuedolycaena*, males may possess or lack a pouch, and if they have a pouch, they apparently may possess or lack androconia (Robbins unpubl.).

### Scent

Many males in the *Atlides* Section of the Eumaeini have odors that are conspicuously perceptible to human beings (Müller 1878, Longstaff 1909, 1912). In the *Atlides* Section, these odors range from “highly floral” in *A. polybe* (Linnaeus) to “imitation grape” in *A. bacis* (Godman & Salvin) while in *Arcas imperialis*, they are “like holding a chocolate bar to your nose” (Robbins unpubl.). Females lack these perceptible odors, and the odor in males fades about 24 h after death. Scent pads appear to be responsible for the odors in male *Atlides* because these males lack other wing scent-disseminating structures, including scent pouches. If live males of *Arcas alleluia* have a perceptible odor, it would indicate that the scent pouches also produce perceptible odors because these males lack scent pads. Lundgren and Bergström (1975) reported bicyclic sesquiterpenes as a pheromone in male lycaenids, but this finding has not been replicated, and the chemical basis of male scents in the *Atlides* Section is yet an open question.

### Genitalia and brush organs

The genitalia of *Arcas* have been well-illustrated (Nicolay 1971), and interspecific differences proposed by Austin and Johnson (1995) were not subsequently corroborated (Bálint 2002). All male *Arcas* have brush organs (terminology from Eliot 1973) attached to the membrane connecting the posterior 8th abdominal segment to the male genitalia vinculum, but again, no interspecific differences have been reported in their structure.

### Habitat

*Arcas* species occur in forest, ranging from undisturbed to moderately disturbed (cf., discussion in Salazar 2009). Most occur in wet forest, but with the exception of

*A. delphia* they may also be found in seasonally dry deciduous forest. *Arcas ducalis* inhabits lowlands and lower montane forest above 1200 m elevation. The *Arcas* species that are unrecorded from lowlands are *A. jivaro* (lower montane forest), *A. gozmanyi* (lower montane forest), *A. splendor* (montane forest) and *A. alleluia* (montane forest).

#### *Larval food plants and immature stages*

Larval food plant families recorded for *Arcas* are Annonaceae (Zikán 1956, Constantino 1997), Lauraceae (data in this paper), and Malvaceae (Janzen & Hallwachs 2010), which includes the traditional plant families Tiliaceae and Bombacaceae, according to the Tropicos database. The larva and pupa of *A. ducalis* have been described (Zikán 1956), with a voucher pupal case in FIOC. Images of the immatures of *A. cypria* and *A. gozmanyi* are available online (Janzen & Hallwachs 2010).

#### *Predation*

The only records of predation on *Arcas* are images of a Mantis (Mantodea) nymph eating an adult male *A. imperialis*, Arraiján, Panamá, 27 November 2011 (courtesy of A. Aiello).

#### *Behavior*

Males set up mating territories, on hilltops or at the edge of forest openings, in the early afternoon, with recorded times from 12:15 to 15:15 h. Accordingly, a pair *in copula* was recorded at 15:30 h. Both sexes of one species were attracted in the early to mid-afternoon to traps baited with decaying fish.

### ***Arcas imperialis* (Cramer)**

#### *Updated taxonomy and nomenclature*

The name *Papilio actaeon* Fabricius had nomenclatural priority over the name *Papilio imperialis* Cramer until the International Commission on Zoological Nomenclature suppressed the former name in 1976 (ICZN opinion 1058, Robbins 2004). Although Nicolay (1971) remarked on the substantial intraspecific — and minimal interspecific — genitalic variation in *Arcas*, Austin and Johnson (1995) described *Arcas magnifica* from males based on different genitalic structures. These differences have not been confirmed, and *A. magnifica* has been treated as a junior synonym of *A. imperialis* (Bálint 2002; Robbins 2004).

#### *Distribution and biogeography*

*Arcas imperialis* is the most widespread species in the genus and is relatively common in forested lowlands. It is recorded from Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, French Guiana, Surinam, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina and Brazil. It inhabits the Transandean, Amazon, and Atlantic Regions. It is sympatric with its sister species, *A. ducalis* (Fig. 35) and with all other *Arcas* species except *A. alleluia*.

### *Elevation and habitat*

*Arcas imperialis* occurs in deciduous and wet forest, including disturbed forest, from sea level to about 1300 m elevation, with literature records as high as 1700 m (Salazar 2009).

### *Larval food plants*

Constantino (1997) recorded a larval foodplant of *A. imperialis* as *Rollinia mucosa* (Jacq.) Baill. (Annonaceae) in Colombia.

### *Male behavior and odor*

Territorial males have been recorded from 12:15 to 14:45 h on eight occasions on four hilltops in the Canal Area, Panama, from September to January (9 vouchers in USNM, 6 males identified by sight by Robbins). Live males were noted to have a chocolate-like fragrance. Territorial males have similarly been recorded on hilltops from 12:15 to 14:00 h in Panama (G.B. Small notes), from 13:00 to 14:30 h in French Guiana (Faynel 2003), and from 12:30 to 14:20 h in Colombia (Salazar 2009).

## ***Arcas ducalis* (Westwood)**

### *Updated taxonomy and nomenclature*

The taxonomy is unchanged since Nicolay (1971).

### *Distribution and biogeography*

*Arcas ducalis* is recorded from the states of Espírito Santo (Brown & Freitas 2000: 86) and Rio de Janeiro south to Rio Grande do Sul, Brazil. It is endemic to the Atlantic Region of Brown (1982). It is sympatric with its sister species, *A. imperialis* (Fig. 35) and with *A. tuneta*.

### *Elevation and habitat and conservation status*

*Arcas ducalis* inhabits wet forest from sea level in the southern part of its range to 1600 m elevation in the north. Following Brown (1993), this species was listed as vulnerable in the states of Paraná and Rio de Janeiro (Casagrande & Mielke 1993, Otero et al. 2000). However, males can be found regularly late in the Brazilian summer on hilltops (see below), and we have seen this species on flowers in downtown Teresópolis (RJ). Mielke and Casagrande (2004) removed *A. ducalis* from the list of vulnerable species in Paraná, an action with which we concur.

### *Larval food plants*

Zikán (1956) found a caterpillar on *Rollinia* (Annonaceae) on 17 May 1921 and gave the common name ‘araticum’, which is used in Brazil for *Rollinia mucosa* (Jacq.) Baill. (Grandtner 2005). It is unclear if the larva was found in Parque Nacional do Itatiaia (RJ) or Passa Quatro (MG). A male, which eclosed on 30 Jul 1921, and its pupal case are deposited in FIOC. Keith Brown also reported oviposition on *Rollinia* in Feb 1988 in Extrema (MG) (pers. comm. to Robbins in April 1991, no voucher).

Herbert Miers reared larvae in Joinville, SC, Brazil on 'canela' (pers. comm. to Robbins in March 1991, no vouchers). Canela means cinnamon and is used in Brazil for a variety of plants in the genus *Nectandra* (Lauraceae) (Grandtner 2005). Keith Brown also reported oviposition on Lauraceae in Feb 1988 in Extrema (MG) (pers. commun. to Robbins in April 1991, no voucher).

#### *Male behavior*

Territorial male behavior in *A. ducalis* has been recorded from 14:14 to 15:15 h on three occasions on two hilltops in southern Brazil in RJ and SC (4 vouchers in USNM).

#### ***Arcas cypria* (Geyer)**

##### *Updated taxonomy and nomenclature*

Other than the addition of *A. publica* Röber to the synonymy of *A. cypria* (Bálint 2002), the taxonomy of this species has been stable.

##### *Distribution and biogeography*

*Arcas cypria* is a relatively common species recorded from Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, northern Colombia and Venezuela. It is endemic to the Transandean Region of Brown (1982). It is sympatric with its sister lineage, *A. ducalis* + *A. imperialis* (Fig. 35), but is sympatric with no other *Arcas* species.

##### *Elevation and habitat*

*Arcas cypria* occurs in deciduous and wet forest at elevations up to 1000 m.

##### *Larval food plants*

Caterpillars have been found on and reared from *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Bombacaceae/Malvaceae), *Luehea seemannii* Triana & Planch. (Tiliaceae/Malvaceae), and *Trichospermum grewiifolium* (A. Rich.) Kosterm. (Tiliaceae/Malvaceae) in the Area de Conservación Guanacaste (ACG), northwestern Costa Rica (Janzen & Hallwachs 2010, adult vouchers 03-SRNP-12974.1, 06-SRNP-30623, 08-SRNP-31887, 08-SRNP-31986 and 08-SRNP-32118 in USNM). The traditional plant families Bombacaceae and Tiliaceae are now considered to be part of the Malvaceae (Tropicos database). Caterpillars are figured (Janzen & Hallwachs 2010).

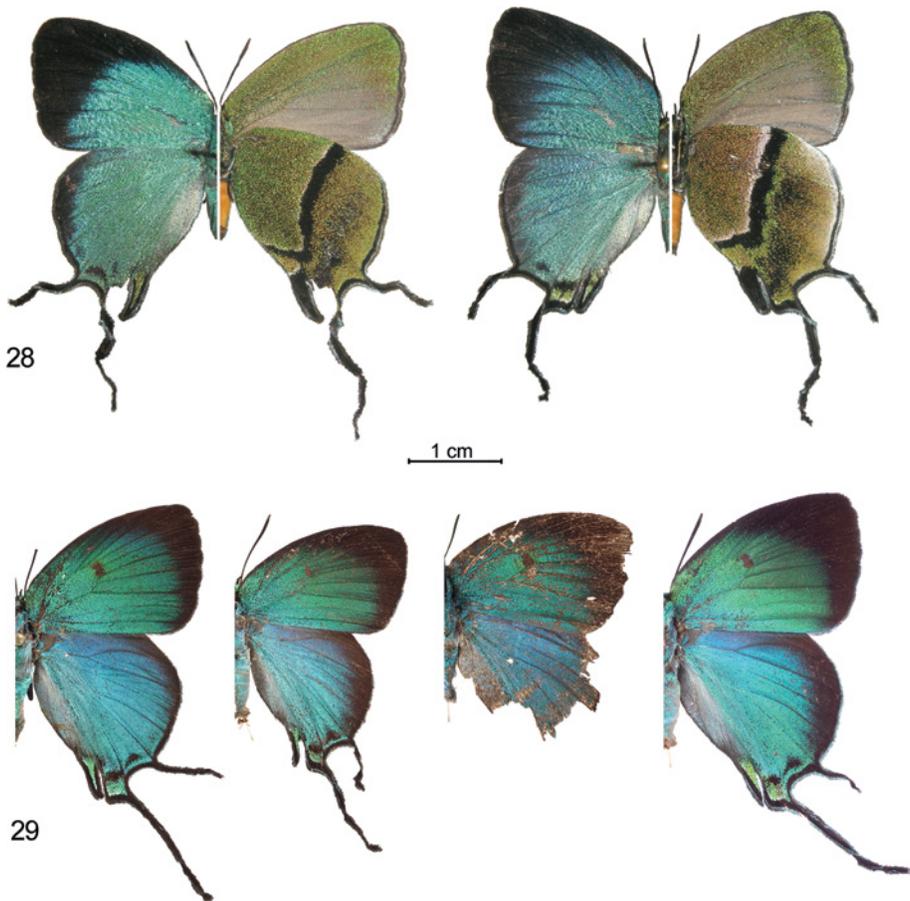
##### *Male behavior*

Males of *A. cypria* have been recorded setting up mating territories from 12:15 to 14:00 h on five occasions on three hilltops in the Canal Area, Panama, throughout the year (7 vouchers in USNM, 1 male identified by sight by Robbins). Most of these males set up mating territories on the same hilltops at the same time as males of *A. imperialis*.

***Arcas jivaro* (Nicolay)***Updated taxonomy and nomenclature*

The wing venation of male *A. jivaro* and *A. delphia* is essentially indistinguishable (Figs 13 and 14), despite different forewing and hindwing male secondary structures. This venation is different from that of other *Arcas* species.

Nicolay (1971) designated a female allotype of *A. jivaro* because it was collected at the same Ecuadorian locality as the male holotype and because *A. tuneta* was unrecorded from Ecuador at that time, but the identity of this specimen was questioned (Bálint 2002). We illustrate females of *A. tuneta* and *A. jivaro* subsequently collected



**Figs 28–29.** (28) Female *A. jivaro* (left) and *A. tuneta* from the same locality, 1100 m, Pastaza, Ecuador. The prominent white scales at the apex of the ventral hindwing in *A. tuneta* are lacking in *A. jivaro*. (29) Non-geographical variation of border width on the dorsal forewings of male *A. tuneta*. From left, Peru (Madre de Dios), Brazil (Santa Catarina), Colombia (Meta), Brazil (Santa Catarina). This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

at one locality in Ecuador (Fig. 28). White scales at the apex on the ventral surface of the hindwing, as occurs in the allotype, are characteristic of both sexes of *A. tuneta* and are lacking in both sexes of *A. jivaro*. However, this issue is nomenclaturally moot because Nicolay designated a male holotype.

#### *Distribution and biogeography*

*Arcas jivaro* is recorded from Ecuador to Bolivia on the eastern slope of the Andes. It is a rare and poorly known species, but appears to be a lower montane species. It is sympatric with *A. tuneta*, which is part of its sister lineage (Fig. 35), and with *A. imperialis*.

#### *Elevation and habitat*

*Arcas jivaro* inhabits wet forest from 800 to 1100 m elevation in eastern Ecuador. A Bolivian male from the Weeks Collection (MCZ) is labeled Chulumani, which is a town at 1650 m elevation, but specimens with this locality label were collected at a variety of elevations in the valley below the town (Weeks 1905).

#### *Male behavior*

One territorial male in eastern Ecuador was collected at 14:45 h on an isolated treetop 10 m above the ground. This tree was located along a stream well below a nearby hill-top (voucher in RCB).

### ***Arcas delphia* (Nicolay)**

#### *Updated taxonomy and nomenclature*

*Arcas katia* Johnson & Salazar is a junior synonym of *A. delphia* (Robbins 2004, Bálint 2006). Bálint (2006: 153) noted that female *A. delphia* has “a faint submedial pattern which appears in most of the specimens I examined as a light band”. This ‘light band’ occurs in all 9 females of *A. delphia* that we examined and in some females of *A. tuneta* (character 10), where the range of variation can be seen in figures 16–18 in Austin & Johnson (1995). Nicolay (1971) noted the close relationship of *A. delphia* with *A. tuneta*.

#### *Distribution and biogeography*

*Arcas delphia* is a relatively uncommon species recorded from the Atlantic slope in Costa Rica and Panama, and from western Colombia and Ecuador. *Arcas delphia* is endemic to the Transandean Region. It is allopatric with its sister species, *A. tuneta* (Fig. 35), and is sympatric with *A. imperiali* and *A. cypria*. It is also sympatric with *A. gozmanyi* in South America, but not in Central America.

#### *Elevation and habitat*

*Arcas delphia* occurs in wet lowland forest under 500 m elevation in Central America. In western Ecuador, it has been found at elevations up to 1100 m.

### *Male behavior*

Males occupy territories in Panama high above the ground from 13:00 to 14:00 h, according to G.B. Small's notes. On the western slope of the Ecuadorian Andes, a territorial male was collected about 6 m above the ground at 13:55 h (voucher in RCB).

### ***Arcas tuneta* (Hewitson)**

#### *Updated taxonomy and nomenclature*

Austin and Johnson (1995) described *A. marginata* and *A. viriditas* from individuals with divergent genitalia, but both names have been placed in the synonymy of *A. tuneta* (Bálint 2002, Robbins 2004).

The females of *A. jivaro* and *A. tuneta* have been confused, as already noted. We illustrate females of each collected on the same hill (Fig. 28).

Nicolay (1971) included populations from both the Amazon Basin and southern Brazil in his concept of *A. tuneta*, but Bálint (2002) made the name *Arcas arcadia* available for specimens from southern Brazil based on (1) a wider dorsal margin on the forewing and hindwing and (2) more gold (as opposed to white) scaling along the "black median band of the hindwing". Nicolay's taxonomy was followed in a checklist (Robbins 2004), but Bálint (2006) reiterated that *A. arcadia* was distinct. We follow Nicolay's taxonomy based on an analysis of how the distinguishing characters mentioned by Bálint (2002) vary. The first character varies substantially in our study series (Fig. 29, figures 3–4 in Austin & Johnson 1995) with a slight clinal tendency towards greater width in the southern parts of its range. However, individuals from the Amazon Basin may have a margin as wide as those from southern Brazil (Fig. 29). The second character varies continuously in our study series from the Amazon Basin from substantial amounts of white to virtually none (figures 7 and 8 in Austin & Johnson 1995 illustrate some of this variation). Individuals from southern Brazil cannot be distinguished by this character.

#### *Distribution and biogeography*

*Arcas tuneta* is a relatively uncommon species, but is widespread. It is recorded from French Guiana, Guyana, eastern Colombia, eastern Ecuador, eastern Peru, and Brazil. *Arcas tuneta* inhabits the Amazon and Atlantic Regions. It is allopatric with its sister species, *A. delphia* (Fig. 35), and is sympatric with *A. imperialis*, *A. ducalis* and *A. jivaro* (Fig. 28).

#### *Elevation and habitat*

*Arcas tuneta* occurs in wet lowland forest from sea level to 1200 m elevation.

#### *Behavior*

On the eastern slope of the Ecuadorian Andes, males were found on 'fish-baited' traps at 14:26 and 15:56 h; females at 12:10, 13:35, 14:35 and 15:22 h (vouchers in RCB). A pair was collected copulating at 15:30 h in eastern Ecuador (vouchers in RCB).

## *Arcas gozmanyi* (Bálint)

### *Updated taxonomy and nomenclature*

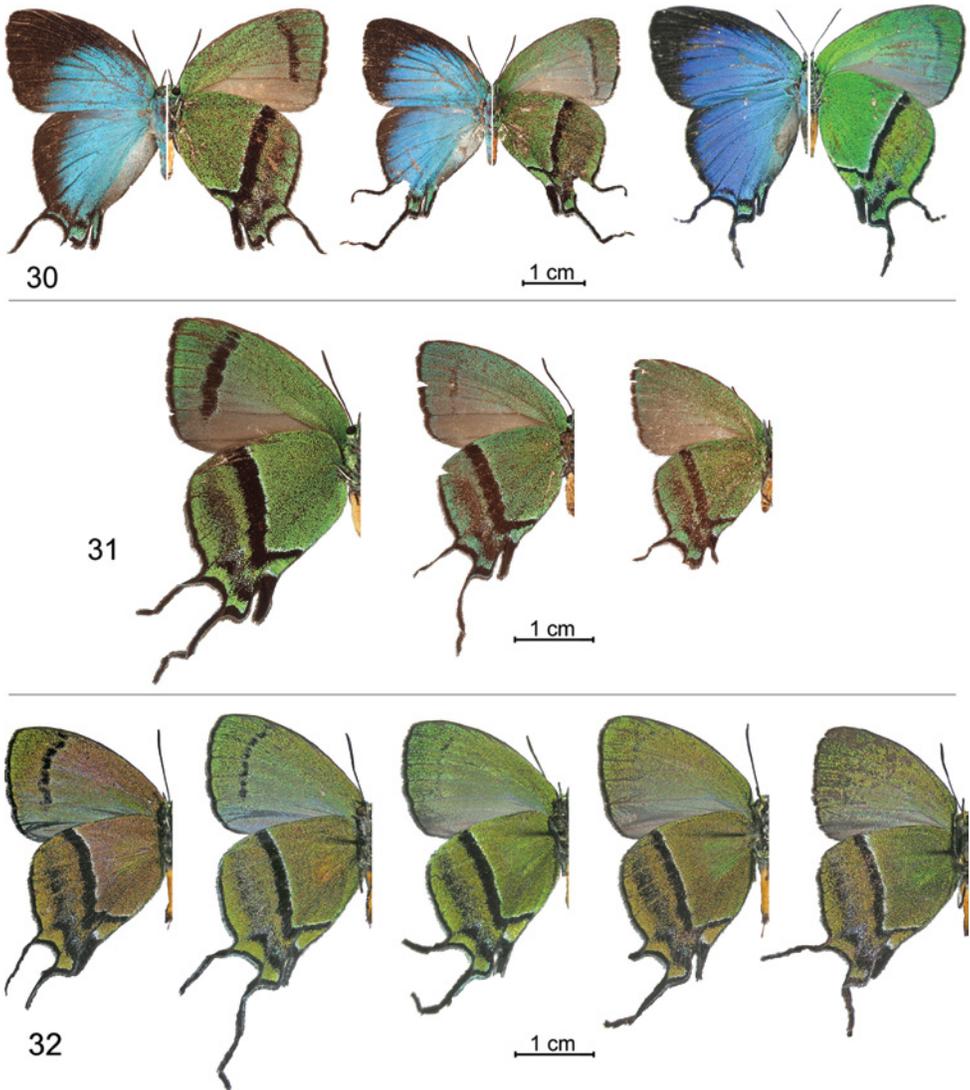
The names *A. splendor*, *A. nicolayi*, *A. lecromi*, *A. gozmanyi* and *A. alleluia* have been confused because the female type of *A. splendor*, the oldest name, has been incorrectly 'identified'. We build the case for the correct species level taxonomy beginning with two observations. The first is that montane females with a black postmedian line on the ventral surface of the forewing, including the holotype of *A. splendor*, occur from Costa Rica to southern Peru near the border with Bolivia (Figs 30 and 34). The second is that there are three distinct montane male phenotypes; a male with a large tear-drop shaped scent pad (*A. gozmanyi* phenotype) (Fig. 25), a male with a medium-sized 'oval' scent pad (*A. splendor* phenotype) (Fig. 26), and a male lacking a scent pad (*A. alleluia* phenotype) (Fig. 27). The range of the montane females with a black postmedian line matches the ranges of the three male phenotypes combined (Figs 33 and 34).

The first question is what are the distributions of the three male phenotypes? Males of the *A. gozmanyi* phenotype occur from Costa Rica to western Colombia and western Ecuador, males of the *A. splendor* phenotype range from western Colombia to eastern Ecuador, and males of the *A. alleluia* phenotype are recorded from two localities in eastern Peru (Fig. 33). Although the first two male phenotypes could possibly be sympatric in western and central Colombia, males of the *A. gozmanyi* phenotype ( $N=29$ ) are not recorded above 1300 m elevation, and males of the *A. splendor* phenotype ( $N=16$ ) are not recorded below 1300 m elevation.

The second question is what females are associated with the *A. gozmanyi*, *A. splendor* and *A. alleluia* male phenotypes? Based on localities where only one male phenotype occurs, we illustrate females from Panama, eastern Ecuador and eastern Peru (Fig. 30) that we consider to be females of the *A. gozmanyi*, *A. splendor* and *A. alleluia* phenotypes, respectively.

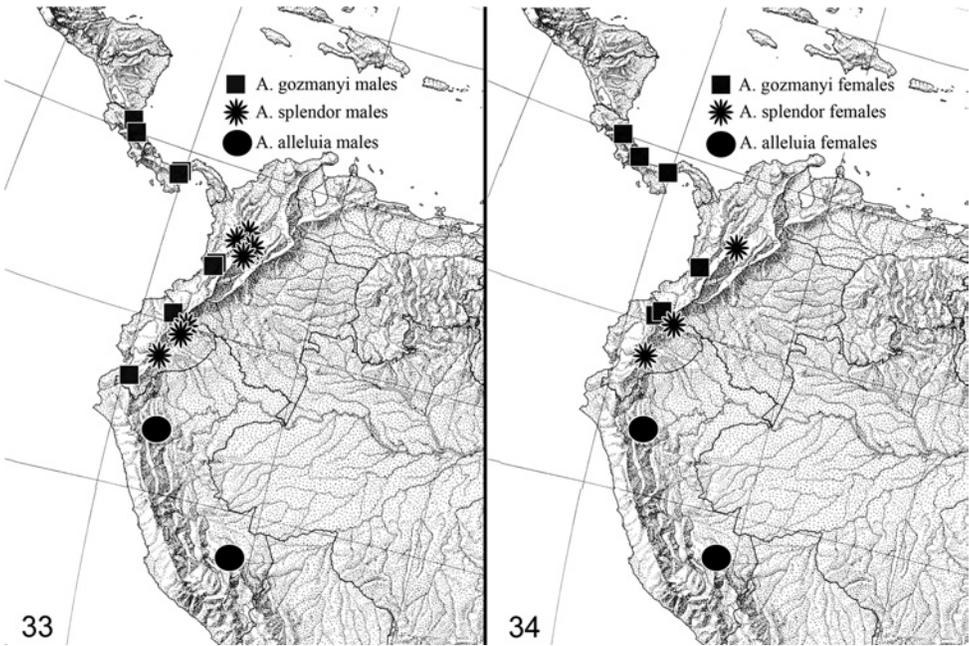
The third question is how are the females of *A. gozmanyi*, *A. splendor* and *A. alleluia* distinguished? To differentiate the females, we measured many aspects of the wings. The proportional width of the dark apical border on the dorsal surface of the forewing along the axis from the base to the apex clearly differentiated females from Central America (*A. gozmanyi*, mean = 0.405, SD = 0.0220,  $N=10$ , 95% confidence limit 0.391–0.420) from those from eastern Ecuador (*A. splendor*, mean = 0.333, SD = 0.0254,  $N=3$ , 95% confidence limit 0.273–0.392), which is a significant difference ( $P < 0.001$ ). The measured proportions in the female holotypes of *A. splendor* (0.344) and *A. alleluia* (0.333) are also significantly different from those of Central American *A. gozmanyi* females. The distribution of males and females of *A. gozmanyi* and *A. splendor* match each other well (Figs 33 and 34). Unfortunately, we were unable to differentiate females of *A. splendor* and *A. alleluia*, and for now, they can be determined only by locality.

Given the answers to the preceding three questions, we can now assign the available names. The name *Arcas gozmanyi* Bálint, 2006 (male type) refers to the species that Nicolay (1971), in part, called *A. splendor*. Based on the distribution of males, *Arcas splendor* (H.H. Druce, 1907) (female type) applies to the species that was subsequently



**Figs 30–32.** (30) Representative females of (from left) *A. gozmanyi* (Panama), *A. splendor* (eastern Ecuador), and *A. alleluia* (eastern Peru). All known females of these species have at least a remnant of a black postmeridian line of the ventral surface of the forewing. The apical border of the forewing on the dorsal surface is wider in *A. gozmanyi* (a statistically significant difference), but indistinguishable in the other two. (31) Size and variation in the expression of the postmedian line on the ventral wing surface in female *A. gozmanyi* from Cerro Campana, Panama. (32) Variation in expression of the postmedian line on the ventral wing surface in male *A. splendor* from two sites in eastern Ecuador. This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

named *Arcas nicolayi* Salazar & Constantino, 1995 (male type) and *Arcas lecromi* Salazar & Constantino, 1995 (male type). Similarly, the name *Arcas alleluia* Bálint, 2002 (female type) applies to the species currently known only from Peru.



**Figs 33–34.** Distribution of *A. gozmanyi* (squares), *A. splendor* (stars) and *A. alleluia* (circles). (33) Males. (34) Females.

A related issue is the correct type locality of *Thecla splendor* Druce. The original description (Druce 1907) gave Colombia as the type locality. There is now a label on the type specimen that says “Colombia, prob. nr. Bogota” (Bálint 2002), which undoubtedly means “Colombia, probably near Bogota”. We do not know who wrote the label or when it was put on the type specimen, but the information on this label is indefinite; the specimen may or may not have been collected near Bogotá. For this reason, the type locality remains Colombia, as in the original description.

#### *Distribution and biogeography*

*Arcas gozmanyi* is recorded from Costa Rica, Panama, western Colombia, and western Ecuador. Although it is an uncommon species in collections, it occurs consistently at some localities such as Cerro Campana, Panama. It occupies the Transandean Region. It is allopatric with the other two species in its ‘trichotomous’ lineage (Fig. 35) and is sympatric with *A. imperialis* and *A. delphia* in South America.

#### *Elevation and habitat*

*Arcas gozmanyi* is recorded from wet lower montane forest from 700–1300 m elevation.

#### *Larval food plants*

A caterpillar was reared from *Hampea appendiculata* (Donn. Sm.) Standl. (Malvaceae) in the Area de Conservación Guanacaste (ACG), northwestern Costa Rica (Janzen &

Hallwachs 2010, adult male voucher 10-SRNP-35334 in USNM). The caterpillar and pupa are figured (Janzen & Hallwachs 2010).

#### *Male behavior*

Males occupy territories from 13:00 to 14:00 h according to G.B. Small's notes.

### ***Arcas splendor* (H.H. Druce)**

#### *Updated taxonomy and nomenclature*

The confusion with *A. nicolayi*, *A. gozmanyi* and *A. alleluia* is detailed above.

#### *Distribution and biogeography*

*Arcas splendor* is recorded from Colombia and eastern Ecuador. Although it is an uncommon species in collections, it occurs consistently at some localities such as Rio Abanico, Ecuador. It occupies the Andean Region. It is allopatric with the other two species in its 'trichotomous' lineage (Fig. 35) and is sympatric only with *A. imperialis*.

#### *Elevation and habitat*

*Arcas splendor* is recorded from wet montane forest from 1300–1800 m elevation.

#### *Larval food plants*

Constantino (1997) listed the larval foodplant of *A. splendor* in Colombia as *Rollinia* (Annonaceae) in a table without further details, but it is unclear if this record refers to *A. splendor* or *A. gozmanyi*. This food plant record needs better documentation.

#### *Male behavior*

Males of *A. splendor* are territorial in eastern Ecuador from 13:17 to 15:15 h (4 vouchers in RCB). According to Salazar (2006), Colombian males are territorial on hilltops from 12:30 to 14:40 h.

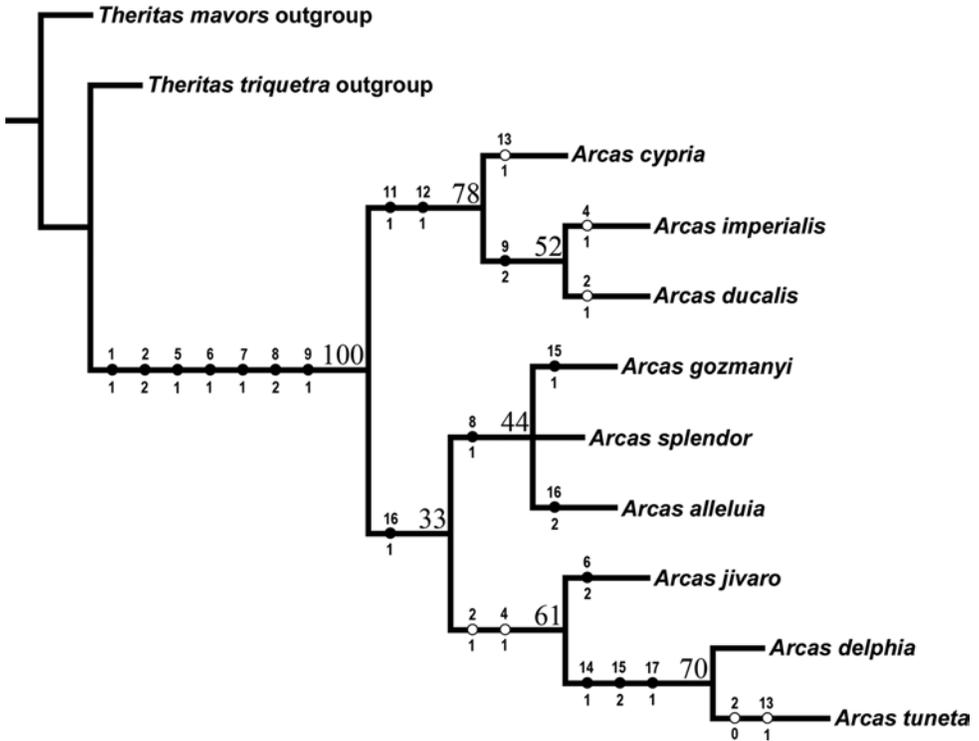
### ***Arcas alleluia* (Bálint)**

#### *Updated taxonomy and nomenclature*

As detailed, the female of *A. alleluia* is indistinguishable from that of *A. splendor* (Fig. 30), but the name is assigned by the locality of the female holotype. A second female that was identified as *A. alleluia* (Bálint 2006) is not identifiable from the illustration.

#### *Distribution and biogeography*

*Arcas alleluia* is known from northern and southern Peru in the Andean Region. It is allopatric with the other two species in its 'trichotomous' lineage (Fig. 35) and is not



**Fig. 35.** Most parsimonious cladogram (28 steps, CI=0.82, RI=0.82) for *Arcas* with character state changes optimized (unambiguous changes only). Bootstrap values at left above the node. All implied weight trees had the same topology.

sympatric with any other *Arcas* species, so far as we are aware. It is yet a rare species in collections.

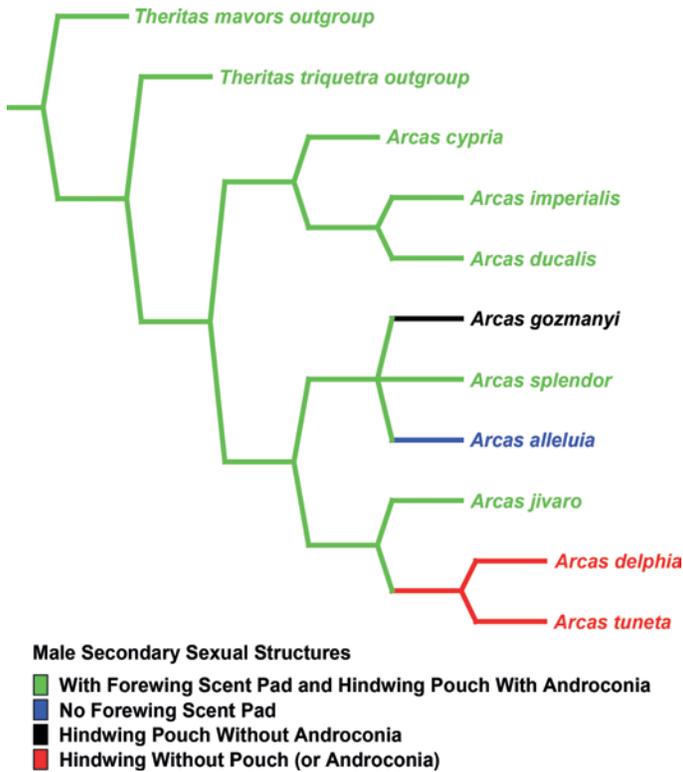
#### *Elevation and habitat*

*Arcas alleluia* occurs in wet forest at elevations from 1600–1900 m.

#### **Phylogenetic analyses**

There was one most parsimonious 28-step equal weight tree with CI=0.82 and RI=0.82 with bootstrap values as noted (Fig. 35). Each implied weight most parsimonious tree with  $K$  varying from 1 to 1000 resulted in one tree with the same topology as the most parsimonious equal weight tree.

The scent pouch on the ventral surface of the hindwing was lost evolutionarily once in the ancestor of *A. delphia* and *A. tuneta* and was not regained (Fig. 36). The specialized scales in this pouch on the ventral surface of the hindwing were lost twice (it is possible that there are vestigial androconia in some specimens of *A. gozmanyi*), and not regained (Fig. 36). Finally, a scent pad was lost once in the ancestor of *A. alleluia* and not regained (Fig. 36). Four *Arcas* species are sympatric with their sister lineage (*A. imperialis*, *A. ducalis*, *A. cypria* and *A. jivaro*) and the other five are not. Five *Arcas*



**Fig. 36.** Cladogram with the presence/absence of scent pouches, androconia on the ventral surface of the hindwing, and scent pads on the dorsal surface of the forewing optimized with unambiguous changes only. This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

species have both scent pouches with androconia and scent pads (*A. imperialis*, *A. ducalis*, *A. cypria*, *A. jivaro* and *A. splendor*) and the other four have only one of these two structures. A contingency table of the two characteristics (Table 3) shows that 8 of 9 species are allopatric and possess one kind of wing androconia or are sympatric and possess two kinds of wing androconia. Among the 200 randomly shuffled terminal taxon trees, the mean number of species that were allopatric and possess one kind of wing androconia plus those that were sympatric and possess two kinds of wing androconia was 4.75, ranging from 2 to 8 species. Three of the trees were 8 (none were 9), so an estimate of the *P*-value is 3/200, or *P*=0.015.

## Discussion

### *Evolution of male secondary sexual organs*

A scent pad or a scent pouch with androconia is lacking in four of nine *Arcas* species (*A. gozmanyi*, *A. alleluia*, *A. delphia* and *A. tuneta*), which is the consequence of three evolutionary losses with no evolutionary gains (Fig. 36). This result is inconsistent with the hypothesis that scent pouches are not lost (Bálint 2006: 149) and with the

hypothesis that regulator genes turn the development of scent-disseminating organs 'on and off' (Burns 1964: 196–197). Although *Arcas* is a small genus, the results of a much larger study (albeit using exemplar taxa) in which phylogenetic relations among 163 eumaeine species were inferred from DNA sequences (Quental 2008) were also inconsistent with the two hypotheses above. While the gene regulator idea is biologically reasonable, we are unaware of evidence from the occurrence of scent pads and scent pouches in the Eumaeini to support it.

Male secondary sexual organs vary conspicuously among *Arcas* species while the genitalia and mating behaviors of *Arcas* appear to be relatively invariant. For example, every male *Arcas* can be distinguished by the shape (including absence), size, color, and location of its scent pad (Figs 19–27). One species lacks a scent pad, two lack a hindwing scent pouch, and one with a pouch lacks androconia. In contrast, the genitalia of *Arcas* do not vary interspecifically (Nicolay 1971). Further, male behavior is very similar among species with males setting up territories from 12:15 to 15:15 h. For example, males of *A. imperialis* set up mating territories on the same hilltops at the same time as males of *A. cypria* (data in this paper) and *A. splendor* (Salazar 2009). These contrasting patterns of variation suggest that the wing secondary sexual organs are responsible in large part for reproductive isolation among sympatric species in *Arcas*.

If male secondary structures are responsible for evolving and maintaining reproductive isolation in phylogenetically close relatives, then these structures might be lost in allopatry because females would not need to distinguish among males of more than one species (Phelan & Baker 1987). They would not be expected to be lost while in sympatry. Further, as noted, a species that loses a male secondary sexual character would be more likely to remain allopatric because it would be less likely to be able to maintain reproductive isolation if it secondarily became sympatric with its closest relatives. Although the evolutionary gain of a male secondary sexual structure is not an issue in *Arcas*, it would be expected to occur during secondary sympatric contact after allopatric speciation or during sympatric speciation.

The results in this paper support the theory just outlined. The four *Arcas* species that lack one kind of wing androconial structure are allopatric with their sister lineage. Four of five *Arcas* species that possess two kinds of wing androconial structures are sympatric with their sister lineage. These results were statistically significant ( $P=0.015$ ) when compared with 200 "random trees" (terminal taxa shuffled). Despite the small number of species in *Arcas*, this result accords with that in moths (Phelan & Baker 1987).

### *Morphology of male scent-disseminating organs*

The male scent-pouch on the ventral surface of the hindwing was discovered over a century ago (Godman and Salvin 1887–1901). The fold in the hindwing between veins  $Cu_2$  and 2A produces a pouch on both the dorsal and ventral surfaces of the hindwing. The ventral pouch contains specialized scales (lacking in *A. gozmanyi*) that are attached to the ventral surface and distal end of the pouch. The ventral part of the pouch in live individuals is flexible, perhaps being functionally analogous to the costal folds of many Lepidoptera (e.g., Burns 1964; Grant 1978). Scent pouches on the

ventral surface of the hindwing between veins  $Cu_2$  and 2A occur in the Eumaeini only in the *Atlides* Section.

Scent pads are distinguished by wing membranes that are separated, forming an internal space — perhaps to retain ‘blood’ after eclosion — with pockets on the dorsal surface that contain secretory cells and the base of an androconium (Thomas 1893; Robbins 1991). The scent pad structure in *Arcas* is the same as that in *Satyrium* Scudder and *Rekoa* Kaye (Thomas 1893; Robbins 1991). Scent pads occur widely in the Eumaeini and Tomarini, but are otherwise unreported in the 31 other tribes of Lycaenidae listed in Eliot (1973) (Robbins & Quental, unpubl.). However, a double scent pad (Character 16), in which the basal one is located at the distal end of the discal cell — distally bordered by the disco-cellular veins — and the distal one is located between veins  $M_1$  and  $M_3$  (occasional exceptions) is unique to the *Atlides* Section.

### *Taxonomic significance of male secondary sexual structures*

Interspecific variation in both male genitalia and male secondary sexual structures is hypothesized to result from sexual selection (e.g., Baker & Cardé 1979; Eberhard 1985). But while insect taxonomists have long used genitalic structures as standard taxonomic characters, the use of male secondary sexual organs above the species level has been varied. For example, Godman and Salvin (1887–1901) placed *Thecla regalis* (Cramer) and *T. coronata* Hewitson in disparate species groups—despite almost indistinguishable wing pattern, venation and genitalia — because the latter species possesses several kinds of male secondary sexual structures that are lacking in the former. The opposing philosophy was proposed by Dixey (1910: cxxxvi), who commented that “... too much dependence must not be placed on the presence or absence of the plume-scales [scent-disseminating scales] as evidence of affinity”. The results in this paper, at least if they are generally applicable, provide (1) an explanation for the repeated observation that male secondary sexual structures may be present or absent in closely related species and (2) in accord with a number of workers (e.g., Dixey 1910; Burns 1964; Birch 1972; Eliot 1973), suggest that the presence and absence of these structures, by itself, is insufficient to infer a lack of relationship.

### **Acknowledgements**

We are grateful to Annette Aiello, Loran Gibson, Gerardo Lamas, Jason Hall, Winnie Hallwachs, Dan Janzen, Mike McInnis and Olaf H.H. Mielke for providing images, data and/or specimens on loan. We acknowledge John Burns and Tiago Quental for discussions on the evolution of male secondary sexual characters and are especially grateful to Keith Willmott for commenting extensively on the manuscript. We thank Ana Maria Velez and Mario Alejandro for kindly obtaining a pdf of an obscure publication. Thanks to the Hennig Society for making TNT software freely available. Vichai Malikul expertly drew a scent pouch, and Karie Darrow made the superb plates. The SEMs were made in the NMNH SEM Lab, for which we thank Scott Whittaker. For financial support Duarte thanks Fundação de Amparo à Pesquisa do Estado de São

Paulo/ FAPESP (grants 02/13898-0, 03/13985-3, 10/14682-8 and 11/50225-3), Pró-Reitoria de Pesquisa da Universidade de São Paulo/USP (Projeto 1), and Conselho Nacional de Desenvolvimento Científico e Tecnológico/CNPq (grants 482816/2009-0 and 563332/2010-7).

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